

TWO NEW BALBARINE KANGAROOS AND LOWER MOLAR EVOLUTION WITHIN THE SUBFAMILY

B.N. COOKE

Cooke, B.N. 1997 06 30: Two new balbarine kangaroos and lower molar evolution within the subfamily. *Memoirs of the Queensland Museum* 41(2):269-280. Brisbane. ISSN 0079-8835.

Lower Jaws and teeth of *Nambaroo couperi* sp. nov. and *Wururoo dayamayi* gen. et sp. nov., fossil balbarine kangaroos from the late Oligocene White Hunter Site of Riversleigh, are described. M₁ trigonid cuspid homology in Hypsiprymnodon is re-interpreted such that a reduced protoconid is recognised, the anterobuccal cuspid is regarded as the protostylid and the anterolingual cuspid as the metaconid. The evolution of lophodont lower molars within Balbarinae is examined on the bases of this interpretation and information supplied by the new species. □ *Riversleigh, kangaroo, Balbarinae, Nambaroo, Wururoo, cuspid homology, lophodonty.*

B.N. Cooke, School of Life Science, Queensland University of Technology, GPO Box 2434, Brisbane, Queensland 4001, Australia; 18 December 1996.

The Balbarinae Flannery, et al., 1982 was erected for a group of fossil macropodids in which the M₁ protolophid is markedly compressed. It assumed phylogenetic significance when Flannery (1989) proposed that balbarines were ancestral to both sthenurines and macropodines.

Balbarines form a major component of the fossil kangaroo fauna of Riversleigh and appear to have had a wide distribution in the Oligocene-Miocene of Australia. Three genera and 8 species have so far been named, but it is more diverse than this. *Balbaroo camfieldensis* Flannery et al., 1982 is known from Bullock Creek and *Balbaroo* sp. Flannery et al. (1982) from the Kangaroo Well Local Fauna, both in the Northern Territory. Three species of *Nambaroo* Flannery & Rich, 1986 were described from the Tarkarooloo Local Fauna of South Australia. Unnamed balbarines have been reported by Flannery (1989) from the Kutjumarpu Local Fauna of South Australia and Woodburne et al. (1993) from the Etadunna Formation of South Australia. Riversleigh balbarines include *Balbaroo gregoriensis* Flannery et al., 1982 and 3 species of *Ganawamaya* Cooke, 1992. The present paper includes descriptions based on lower jaws and teeth of a new species of *Nambaroo* and a new genus and species of balbarine.

METHODS

Molar homology follows Lockett (1993). Premolar homology follows Flower (1867). Homology of molar structures has been determined by reference to a generalised tribosphenic pattern,

outlined by Szalay (1969), following Ride (1993). Terminology follows Van Valen (1966), Szalay (1969) and Butler (1990). However, the 'anterior cingulid' is restricted in use to that component of the macropodoid lower molar anterior cingular shelf lying lingual to the anteriorly directed paracristid. 'Prectingulid' is refers to that component lying buccal to the paracristid. Van Valen (1966, 1994) used 'precingulid' for the anterior cingular shelf anterobuccal to the paracristid of plesiomorphic mammalian lower molars. The distinction is made here because lingual and buccal components of the macropodoid anterior cingular shelf are demonstrably of different origins. The buccal component is the more plesiomorphic since it occurs in plesiomorphic balbarines such as *Nambaroo couperi* sp. nov. More derived balbarines such as *Wururoo* gen. nov. and *Balbaroo* demonstrate the development of the neomorphic lingual component via lingual displacement of the paraconid and lingual extension of the paracristid. Suprageneric classification follows Aplin & Archer (1987). QMF denotes Queensland Museum fossil collection catalogue numbers. Measurements are in millimetres.

SYSTEMATICS

Family MACROPODIDAE Gray, 1821
Subfamily BALBARINAE Flannery,
Archer & Plane, 1982
Nambaroo Flannery & Rich, 1986

Nambaroo couperi sp. nov.
(Figs 1, 2, 5A; Table 1)

DIAGNOSIS. *Nambaroo* with a hypoconulid at the posterior, buccal base of the entoconid on M₁ and marked convexities along the lateral margins adjacent to the ends of the interlophid valley on all lower molars except M₄.

MATERIAL. Holotype QMF30401, a partial right dentary consisting of the entire horizontal ramus, most of the angular process and portion of the ascending ramus to the level of the damaged condyle. P₃ and M₁₋₄ are preserved; from White Hunter Site, Hal's Hill, D Site Plateau, which has been correlated (Myers & Archer, this volume) with the Ngama Local Fauna from the Tirari Desert which Woodburne et al. (1993) have shown to be late Oligocene, about 24 to 26My.

ETYMOLOGY. For Patrick Couper, Queensland Museum, for his assistance during the course of this research.

DESCRIPTION. The holotype is a fragment of a right dentary consisting of the entire horizontal ramus, most of the angular process and portion of the ascending ramus to the level of the damaged condyle (Fig. 1 A, B). Dorsal edge of the diastema delineated by a ridge with matrix-filled alveolus for a very small I₂ or analogous tooth at anterior end. Horizontal ramus twisted, with mesial surface inclined slightly dorsally below P₃ and slightly ventrally below M₄. Mandibular symphysis extending as far posteriorly as the level of the anterior margin of P₃. On the buccal surface the anterior mental foramen located below and slightly anterior to P₃, with a much smaller posterior mental foramen below the hypolophid of M₂. Horizontal ramus deepest below M₁, with its zone of most ventral protrusion below M₃. Ventral margin straightest below P₃-M₃, curving upwards below the diastema and more steeply so posterior to M₃. Buccal margin of the masseteric fossa straight so that the entrance to the masseteric canal is 'D' shaped in cross section. Ventral margin of the masseteric fossa low on the ramus, well below the level of the molar row. Inferior dental canal recessed into the lingual wall of the masseteric canal but not partitioned from it. Because of the confluence of the two canals, forward extent of the penetration of the masseter difficult to determine, but the gradient of anterior canal constriction suggesting insertion no further forward than M₃. Lingual border of the angular process in the same vertical plane as the lingual margin of the horizontal ramus but the angular process extending more posteriorly than the

ramus. Large portion of the floor of the pterygoid fossa lost.

Ascending ramus rising at 100° relative to the plane of the molar row. Condyle situated 9.4mm above the molar row, a transversely elongate structure, broader lingually, tapering to the buccal side, obliquely inclined to the plane of the ascending ramus.

Dentition. Molar row straight in both occlusal and lateral view. P₃ flexed slightly buccally out of alignment with molar row. Occlusal surfaces of anterior molar lophids inclined slightly buccally. Those of more central molars more or less horizontal. Hypolophid of M₄ inclined lingually. Slight increase in molar size posteriorly.

P₃ gracile, short and blade-like with horizontal occlusal margin. In occlusal view with an elliptical outline with the occlusal crest occupying approximate midline, although curving lingually posteriorly. Five cuspids, of which most posterior largest, occupying the occlusal crest. Lingual and buccal transcrisids associated with each cuspid, although those on lingual surface partly obscured by wear. Anterior and posterior margins of crown delineated by vertical cristids.

In occlusal view M₁ with a rounded anterior margin and lateral convexities low on the crown adjacent to the ends of interlophid valley. Proto-lophid shorter than hypolophid; protoconid positioned on approximate midline of tooth. Protoconid taller than metaconid, buttressed buccally by a protostylid about same height as metaconid. Paracristid running almost directly forward to anterior margin where it meets anterior edge of a precingulid which descends steeply to buccal margin of tooth. No anterior cingulid, trigonid basin open anterolingually. Cristid obliqua inclined slightly lingually, descending anterior face of the hypoconid, turning anteriorly to cross interlophid valley and terminating at base of protostylid.

Entoconid taller than hypoconid. Occlusal crest of hypolophid forming shallow 'V' with lingual arm steeper than buccal. Low point of hypolophid slightly lingual of midline. Preatocristid descending to interlophid valley floor from apex of entoconid. Wedge shaped prominence at posterior base of entoconid, interpreted here as a hypoconulid because its position corresponding to that occupied by hypoconulid in other marsupials and, as in these animals, contacted by the posthypocristid. Short, lingually displaced, diagonal posthypocristid and hypoconulid forming posterobuccal border of small fossette in poste-

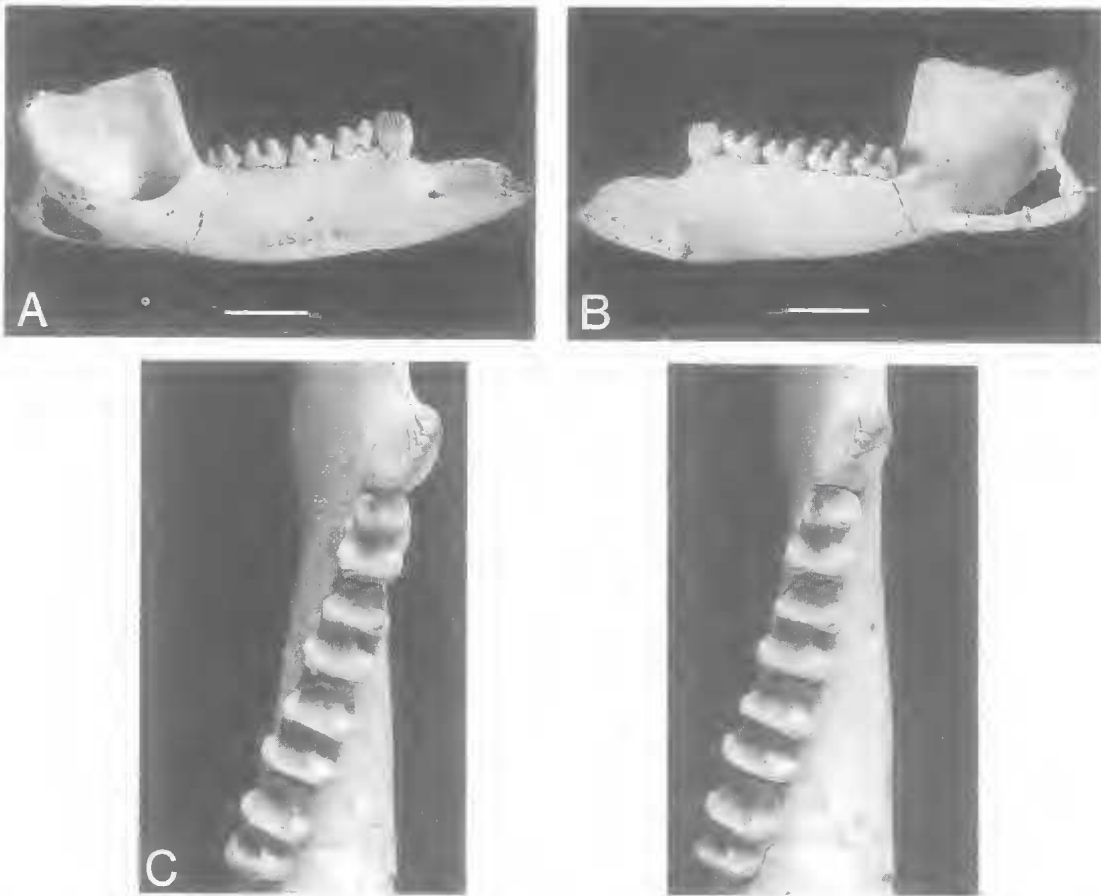


FIG. 1. QMF30401, Holotype of *Nambaroo couperi* sp. nov. A, buccal view. B, lingual view. C, stereopair of occlusal view. Scales = 10mm.

rior face of entoconid. Rounded, lingual border probably representing postentocristid. From base of hypoconulid a hypocingulid extending across about half width of posterior base of hypolophid.

M₂ larger than M₁, approximately rectangular in outline, but with lateral convexities of crown base adjacent to ends of interlophid valley. Protolophid and hypolophid about equal in length, lingual cuspids taller than buccal cuspids. Occlusal margins of both lophids shallowly concave. Paracristid running anterolingually to anterior margin from which enamel has been lost, although sufficient remains to indicate that an anterior cingulid ran between paracristid and lingually positioned premetacristid. Short, steeply sloping precingulid extending from anterior end of paracristid to buccal margin of the tooth. Cristid obliqua running anterolingually across interlophid valley to join posterior base of pro-

tolophid at about midline. Preentocristid short, not reaching floor of interlophid valley. Postentocristid running vertically down posterior, lingual edge of entoconid to meet low and somewhat irregular hypocingulid which runs transversely across half width of the posterior face of hypolophid. No posthypocristid.

M₃ similar to M₂ but metaconid and hypoconid more nearly equal in height, hypocingulid less developed and cristid obliqua interrupted adjacent to base of protolophid.

M₄ differing from more anterior molars in the following: protolophid longer than hypolophid; no obvious convexities of crown base adjacent to ends of the interlophid valley; some wrinkling of the enamel within trigonid basin; precingulid less obvious; rounded postmetacristid descends posterior face of metaconid to floor of interlophid valley; cristid obliqua interrupted before contact-

TABLE 1. Dental parameters for QMF303401, Holotype of *Nambaroo couperi* sp. nov.

Cat. No.	P3			M ₁			M ₂			M ₃			M ₄		
	l	mw	h	l	pw	hw	l	pw	hw	l	pw	hw	l	pw	hw
QMF30401	5.2	2.9	3.9	5.2	2.6	3.3	5.4	3.5	3.9	5.6	3.9	4.1	5.4	3.8	3.6

ing base of protolophid and ridge of enamel runs transversely across floor of the interlophid valley from anterior end of cristid obliqua to buccal margin; hypoconid taller than entoconid (which is slightly damaged); no distinct postentocristid; hypocingulid in form of rounded, transverse prominence crossing posterior face of hypolophid.

DISCUSSION. *N. couperi* is similar in size to *N. saltavus*, *N. tarrinyeri* and *N. novus* which were described by Flannery & Rich (1986) from the Tarkarooloo Local Fauna of South Australia. Apart from the plesiomorphic hypoconulid, *N. couperi* is in other aspects of talonid morphology, more derived than *N. saltavus*. It lacks a postentocristid which is present in *N. saltavus*, and has a well-developed hypocingulid crossing buccally from the hypoconulid on the posterior base of the hypolophid, present also in *N. tarrinyeri* and *N. novus* but undeveloped in *N. saltavus*. The M₁ cristid obliqua contacts the protostylid of *N. couperi* as it does in *N. saltavus*, a condition which Flannery & Rich (1986) considered plesiomorphic for macropodoids. In *N. novus* the cristid obliqua contacts the base of the protoconid and in *N. tarrinyeri* the cristid obliqua

bifurcates and contacts both protostylid and protoconid. M₁ trigonid morphology in *N. couperi* is most similar to *N. novus* in that both have an anteriorly directed paracristid, lack a paraconid and have a protostylid which is closely associated with the protoconid.

Wururoo gen. nov.

TYPE SPECIES. *Wururoo dayamayi* sp. nov.

DIAGNOSIS. Balbarines with a large, trenchant P3 and a posterobuccally inclined enamel ridge (the 'protostylid crest') descending from the apex of the protoconid of M₁.

ETYMOLOGY. Gulf coast aboriginal *wuru*, a long time ago (Breen, 1981), and *roo* a common Australian diminutive for 'kangaroo'. Masculine.

Wururoo dayamayi sp. nov. (Figs 3, 4, 5B; Table 2)

DIAGNOSIS. As for genus.

MATERIAL. Holotype QMF19820. A fragment of the horizontal ramus of a right dentary, extending from the anterior end of the diastema to the posterior of the molar row and preserving P3 and M₁₋₄ from White Hunter Site, Hal's Hill, D Site Plateau, which has been correlated (Myers & Archer, 1997) with the Ngama Local Fauna from the Tirari Desert which Woodburne et al. (1993) have shown to be late Oligocene, about 24 to 26My.

ETYMOLOGY. Waanyi *daya*, chop; *mayi* tooth, for the tall, robust plagiulacoid premolar of the holotype.

DESCRIPTION. Only small portion of anterior margin of ascending ramus present, remainder of dentary posterior to M₄ lost. Horizontal ramus deepest below M₃/M₄, tapering gently anteriorly, ramus twisted so that mesial face inclines dorsally below P3 and slightly ventrally below M₄. Low ridge running length of dorsal margin of very short diastema. Mental foramen well below and slightly anterior to P3, small posterior mental foramen below hypolophid of M₂. Masseteric canal elliptical in cross section, extending forward at least as far as anterior of M₂, from which position anterior of canal blocked by undissolved

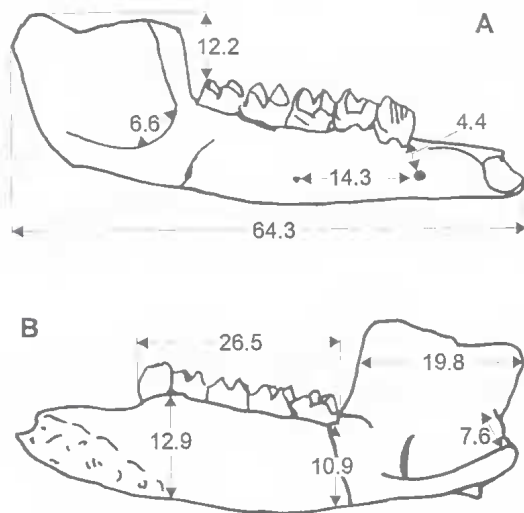


FIG. 2. Dimensions of QMF30401, holotype of *Nambaroo couperi* sp. nov. A, buccal view. B, lingual view.

matrix. A narrow canal, the inferior dental canal or branch thereof, partitioned from lingual side of masseteric canal by thin lamina of bone anterior to M₄. Mandibular symphysis extending posteriorly to below mid point of P₃. Molar row concave in lateral view and straight in occlusal view. Molar size increasing from M₁ to M₃ but M₄ a little smaller than M₃.

Dentition. P₃ large, robust, plagiolacoid, occlusal edge well above occlusal plane of molar row, long axis flexed slightly buccally out of alignment with line of molar row. Viewed occlusally with a convex buccal margin and slightly concave lingual margin. Lingual face of crown inclined at steeper angle than is buccal. Occlusal margin on approximate midline for most of length, but slightly lingually displaced at posterior end. Six cuspids on occlusal margin, all but most posterior having associated lingual and buccal transcrisrids. Cristids descending anterior and posterior margins of crown from corresponding cuspids.

M₁ roughly rectangular in occlusal outline but with distinct lingual convexity in crown base adjacent to interlophid valley. Anterior margin abutting posterior buccal margin of P₃. Protolophid markedly shorter than hypolophid with protoconid set on approximate midline. Lingual cuspids positioned closer to margin and with steeper lateral walls than buccal cuspids. Both protolophid and hypolophid crests concave anteriorly, posterior faces of both lophids vertical. Protoconid taller than metaconid. Paracristid straight but anterolingually inclined as descends from protoconid apex to a prominence positioned just posterior to anterior margin. A short but clearly defined ridge is directed lingually from apex of prominence, ending abruptly anterior to midpoint of protolophid. While the prominence may represent the paraconid, an alternative view preferred here is that this ridge represents a lingual extension of the paracristid, and its termination the paraconid (see Fig. 7c). Line of paracristid continued by a ridge running anteriorly from anterior prominence for very short distance and at steeper angle to anterior margin. From here a continuous ridge descends ventrobuccally on anterior margin, forming border of narrow precingulid which ends before reaching buccal margin. No premetacristid or postmetacristid. An enamel ridge, the 'protostylid crest' descends posterobuccally from apex of protoconid for about half height of that cusp where it is contacted by ascending, anterior

portion of cristid obliqua. Cristid obliqua descends anterolingually from apex of hypoconid before turning anteriorly to cross wide interlophid valley and ascend diagonally on posterior of protoconid.

Entoconid taller than hypoconid which shows evidence of wear: enamel breached on lingual side of apex. Preentocristid descends directly anteriorly from apex of entoconid to floor of interlophid valley. Posthypocristid short, extremely lingually displaced, originating at lowest point of hypolophid crest, closer to entoconid than hypoconid, descending ventrolingually to meet postentocristid just above base of entoconid. Inverted triangular fossette enclosed laterally by posthypocristid and postentocristid. Below junction of postentocristid and posthypocristid is short, prominent enamel ridge, descending at different angle to postentocristid and which may represent a reduced hypoconulid. This ridge forms lingual margin of broad, horizontal hypocingulid extending across two-thirds of base of hypolophid.

Broad wear facets on posterior face of protolophid extend across link between protostylid crest and cristid obliqua; similar facets on posterior face of hypolophid extend across posthypocristid. Facets bear fine vertical striae.

M₂ rectangular in occlusal outline but with slight concavity of lingual margin adjacent to end of interlophid valley. Protolophid and hypolophid subequal in length, occlusal crest of hypolophid slightly more anteriorly concave than that of protolophid. Lingual cuspids set closer to lateral margin and with steeper lateral walls than buccal cuspids. Metaconid taller than protoconid which shows evidence of wear: enamel breached lingually adjacent to apex. Paracristid directed anterolingually as descends from protoconid apex to anterior margin. Prominent premetacristid runs slightly buccally as descends from metaconid apex to anterior margin. Short, broad anterior cingulid enclosed between these cristids. Short precingulid buccal to paracristid. In posterior view occlusal crest of protolophid forms shallow 'V' with low point located closer to protoconid than metaconid. Cristid obliqua forms thick enamel ridge as crosses interlophid valley, tapering somewhat anteriorly as ascends short distance on lingual side of posterior face of protoconid. No postmetacristid or preentocristid: broad interlophid valley widely open lingually. Floor of interlophid valley considerably more elevated on lingual side of cristid obliqua than on buccal side which slopes steeply towards crown

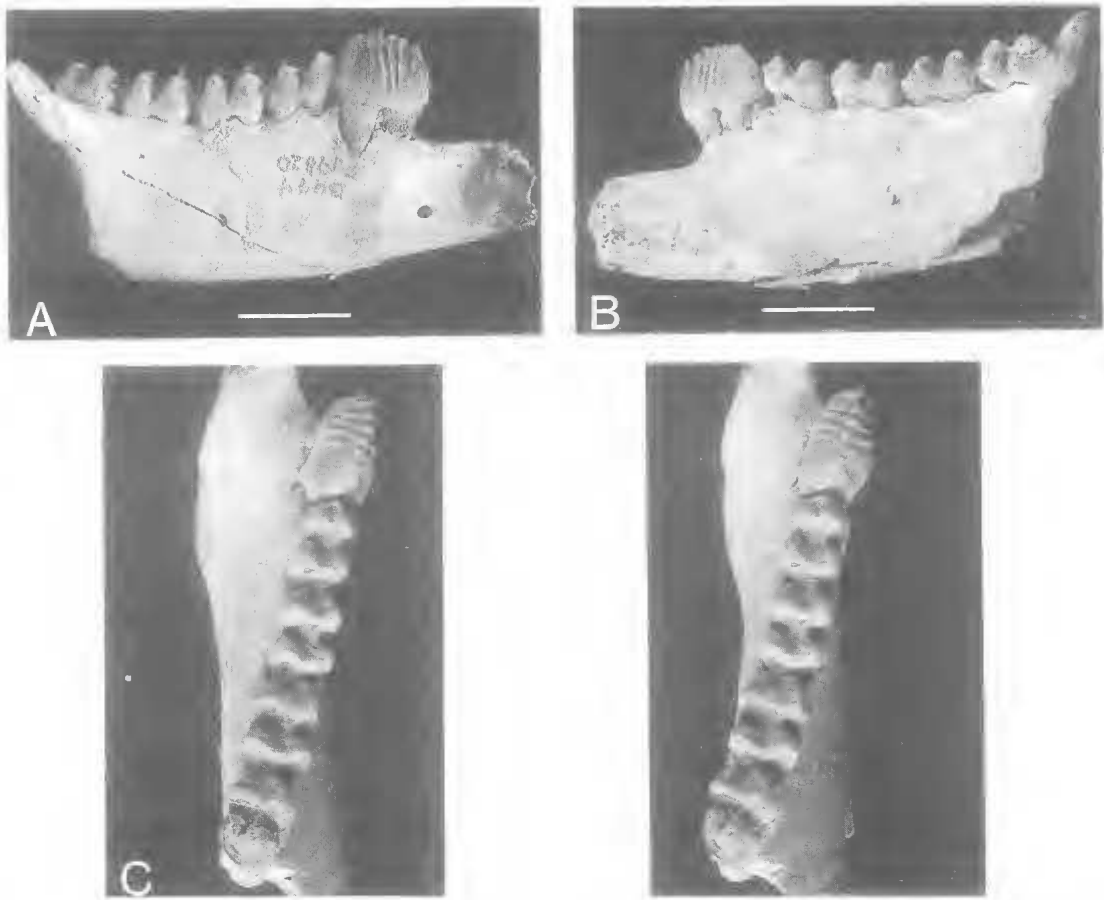


FIG. 3. QMF19820, Holotype of *Wururoo dayamayi* gen. et sp. nov. A, buccal view. B, lingual view. C, stereopair of occlusal view. Scales = 10mm. AR number is an informal system used in the Vertebrate Palaeontology Laboratory, University of New South Wales.

base. Entoconid and hypoconid subequal in height. No posthypocristid. Thick ridge of postentocristid continuous with similarly prominent hypocingulid which descends slightly ventrally as crosses posterior base of the hypolophid.

M₃ with longer anterior cingulid, lingual cusps taller than buccal cusps, protolophid slightly longer than hypolophid and thickened ridge, representing remnant of posthypocristid, descending vertically from low point of occlusal crest on posterior face of hypolophid. Less worn than is M₂. Cristid obliqua can be seen to arise from more anterolingual position relative to apex of the hypoconid.

M₄ smaller than M₃ with much narrower anterior cingulid. Lacking precingulid buccal to paracristid. Hypolophid markedly shorter than protolophid. Metaconid taller than protoconid, crest of protolophid formed chiefly by buccal

crest from apex of metaconid, descending to meet lingual flank of protoconid at a point directly in line with anterior end of cristid obliqua. Cristid obliqua originates lingual to hypoconid apex and runs directly anteriorly across interlophid valley. Hypoconid and entoconid subequal in height but entoconid set somewhat anterior to hypoconid. Apex of entoconid damaged during life and broken edges of enamel subsequently smoothed as a result of wear. Hypolophid crest with a narrow V-shape in posterior view with lingual arm running slightly anteriorly towards damaged apex of entoconid. No preentocristid but very thick postentocristid running ventrobuccally on posterior face of entoconid, merging with equally prominent hypocingulid which crosses half width of hypolophid base.

TABLE 2. Dental parameters for QMF19820, Holotype of *Wururoo dayamayi* gen. et sp. nov.

Cat. No.	P ₃			M ₁			M ₂			M ₃			M ₄		
	l	mw	h	l	pw	hw	l	pw	hw	l	pw	hw	l	pw	hw
QMF19820	8.6	4.9	6.7	5.9	4.1	4.2	6.5	4.8	4.5	6.9	5.1	4.7	6.7	4.3	4.1

DISCUSSION. P₃ is much larger and more massive than that in *Nambaroo* or *Ganawamaya* Cooke, 1992, and is similar to that in undescribed Riversleigh species of *Balbaroo*. The large P₃ in the latter balbarines is more similar in profile and size relative to molars to propleopines and hypsiprimnodontines than to macropodids. The diastema in *W. dayamayi* is also much shorter than in *Nambaroo* or *Ganawamaya*. The shorter diastema and markedly more robust P₃ may be indicative of a greater reliance on the use of premolar shearing action in food collection and/or processing. The similarity of plagiulacoid premolars in more derived balbarines, propleopines and hypsiprimnodontines may be the result of convergence in species placing a similar emphasis on premolar shearing. However, premolars in these groups are similar in form to those of phalangerids and it is likely that the plagiulacoid premolar form is plesiomorphic for macropodoids. If robust, plagiulacoid premolars are plesiomorphic, within Balbarinae the markedly more gracile premolars of *Nambaroo* and *Ganawamaya* would represent an apomorphy for a clade containing these two genera.

The lingually displaced M₁ posthypocristid seen in *W. dayamayi* is also present in species of *Nambaroo* and in *Ganawamaya aediculis* Cooke, 1992. Its widespread occurrence among plesiomorphic balbarines supports the view of Flannery & Rich (1986), that lingual displacement of the posthypocristid has played an important role in hypolophid formation in Balbarinae. The connection of the cristid obliqua to the pro-

styloid crest resembles the connection between the cristid obliqua and the discrete prostyloid of *Nambaroo saltavus* as noted by Flannery & Rich (1986), and suggested by them to represent the plesiomorphic state of this character in macropodids.

The M₁ precingulid in other undescribed plesiomorphic balbarine species (pers. obs.) receives the posterolingual cusplule of P₃. The precingulid is low in *W. dayamayi*, suggesting that a prominent posterolingual cuspid is to be expected on its P₃. The lingual ridge associated with the M₁ paraconid forms the margin of a small anterior cingulid which receives the posterior end of the P₃ occlusal margin, as indicated by signs of wear on the posterior face of the ridge. The broad wear facets on the posterior faces of the M₁ lophids indicate broad contact with the lophes of M¹ while the orientation of the striae indicate greater vertical rather than lateral relative movement between lophes and lophids.

CUSPID HOMOLOGY AND EVOLUTION OF LOWER MOLAR MORPHOLOGY IN BALBARINAE

Differing views of cuspid homology and evolution of lower molar morphology among macropodoids are examined and alternative hypotheses proposed to determine homology of structures on lower molars of plesiomorphic balbarines from Riversleigh and to elucidate the course of molar evolution within Balbarinae. Since interpretations of cuspid homology in *Hypsiprymnodon* have been central to wider arguments pertaining to macropodoid molar evolution, such interpretations of previous authors are reviewed first and a new interpretation presented which incorporates evidence provided by the new species described herein.

The posterobuccal prostyloid crest in *W. dayamayi* is very similar to that which descends from the dominant trigonid cuspid to a tiny buccal cuspid in dP₃ of *Hypsiprymnodon moschatus*. Ride (1961) identified the dominant cuspid as the metaconid and the tiny cuspid as the protoconid, but has since modified this interpretation (Ride, 1993), considering the central trigonid cuspid posterior to the paraconid on dP₃ to be a

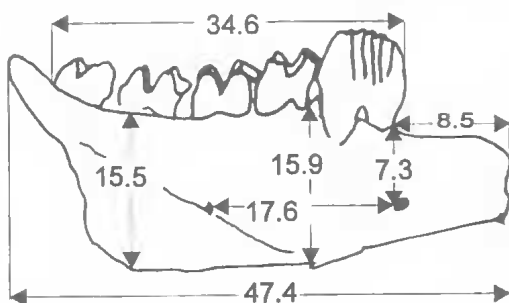


FIG. 4. Dimensions of QMF19820, holotype of *Wururoo dayamayi* gen. et sp. nov., buccal view.

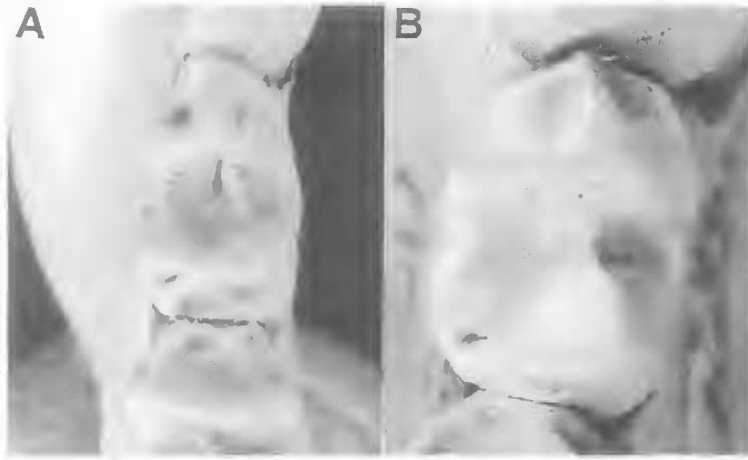


FIG. 5. Posterior occlusal views of M_1 . A, QMF303401, holotype of *Nambaroo couperi* sp. nov. B, QMF19820, holotype of *Wururoo dayamayi* gen. et sp. nov..

parametaconid and the small cuspid posterobuccal to this to be the protoconid, with the normal relationship of protoconid, metaconid and paraconid preserved on M_1 , the parametaconid having been lost in this tooth.

Archer (1978) raised the possibility that the anterobuccal cusp in M_1 (his M_2) of *H. moschatus* (and other macropodoids) may be 'the homologue of the phascolarctid protostylid and not the protoconid' and further that 'the tiny cusp observed by Ride (1961) on M_1 (Ride's dP_4 and here dP_3) of *Hypsiprinmodon* may be the serial homologue of this protostylid'. Archer & Flannery (1985) and Flannery & Rich (1986) also identified the posterobuccal cuspid of the M_1 trigonid of *H. moschatus* as the protostylid having here an anterior cristid descending to the anterior margin, and the cuspid lingual to this, also with an anterior cristid, as the protoconid, the metaconid being displaced posterolingually.

The interpretation of trigonid cuspid homology on dP_3 offered by Archer (1978) is accepted here but none of the above views regarding M_1 trigonid morphology in *H. moschatus* are upheld. For reasons explained below, the most buccal cuspid-like structure associated with the protolophid is accepted as the protostylid but the lingual cuspid of the protolophid is regarded as the metaconid.

As Ride (1993) noted, constraints imposed by functional interactions with premolars can alter the topography of teeth at the premolar/molar boundary, so cuspid homology of M_1 in *H. moschatus* has been examined with reference to

more posterior molars. Molars posterior to M_1 have a buccally positioned protoconid which has a paracristid running to the anterior margin. The metaconid of these molars is lingually positioned and has an associated premetacristid. Both cristids are present on M_1 and bear the same relationship to each other as they do on more posterior molars. The metaconid is distinct but the protoconid, from which the paracristid originates, may be considerably reduced and is more centrally positioned, the trigonid thereby becoming laterally compressed in a manner closely resembling that seen in *balbarines*. In unworn *H.*

moschatus specimens (QMJ10233, QMJ9327, QMJ145), the paracristid originates from a slight elevation, interpreted here as the reduced protoconid (Fig. 6F). A posterobuccal crest links this to a larger cuspid which is thus the protostylid in the sense in which the term is used by Van Valen (1966), and Butler (1978): it occurs in the same position as the protostylid of other diprotodont marsupials, e.g., pseudocheirids and phascolarctids and *Nambaroo*, a position in which it fulfils the function ascribed to it by Butler (1978), i. e., 'to shear against the anterolingual surface of the paracone of the corresponding upper tooth' (a function which could not be fulfilled by the 'one or more protostylids' indicated by Ride (1993), as occurring on the precingulid anterobuccal to the M_1 trigonid in the propleopines, *Jackmahoneya* and *Propleopus*).

Ride (1993) indicated 3 cuspid immediately posterior to the paraconid of dP_3 of *H. moschatus*: the large, central cuspid identified as the parametaconid, a posterolingual metaconid and a very small posterobuccal protoconid. The posterolingual cuspid is accepted here as the metaconid but since the large, central cuspid has a cristid running anteriorly from its apex toward the paraconid, the cuspid is here regarded (as it was by Archer, 1978) as the protoconid, its cristid as the paracristid and the small posterobuccal cuspid as the protostylid, homologous with that which also occurs on dP_3 in undescribed Riversleigh specimens of *Nambaroo* (pers. obs.), the protostylid on M_1 of *H. moschatus* and the

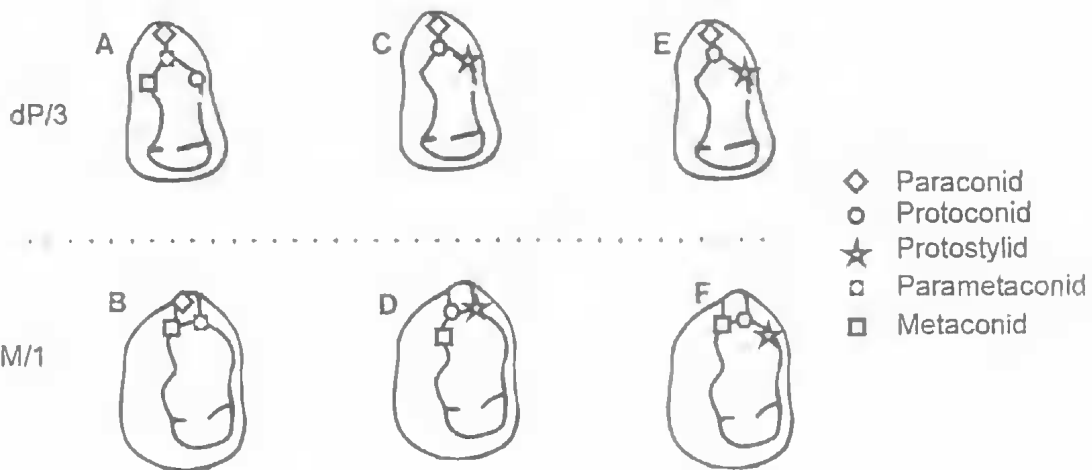


FIG. 6. Interpretations of trigonid cuspid homology in *Hypsiprymnodon moschatus*. A & B, Ride (1993). C, Archer (1978). D, Archer & Flannery (1985). E, F, Cooke (therein).

protostylid crest on M_1 of *Wururoo* and on dP_3 of bulungamayine species (Cooke, 1997).

The homology of the buccal cuspid on the M_1 protolophid of propleopines is less clear. Ride (1993) labelled this cuspid as the protoconid and the cuspid immediately lingual to it as a neomorph, the parametaconid. Flannery & Archer (1985) labelled the buccal cuspid as the protostylid and the cuspid immediately lingual to it as the protoconid. While it is clear that the protostylid, as a discrete cuspid or as a protostylid crest, is common among plesiomorphic macropodoids, it is unusual in this group for it to have acquired a cristid mimicking the paracristid in linking to the anterior cingulid. If Flannery & Archer are correct, this would constitute a synapomorphy for propleopines as would the neomorphic parametaconid in the interpretation of Ride.

The suggestion of Archer & Flannery (1985) that the buccal cuspid of the protolophid in M_1 of propleopines and potoroines was the protostylid and that the metaconid was lost in potoroines but retained in propleopines was enlarged upon by Flannery & Rich (1986). They suggested that in potoroines the protostylid formed the buccal protolophid cuspid and the protoconid the lingual cuspid, in contradistinction to macropodids in which the protostylid is lost and the buccal cuspid is the protoconid and the lingual cuspid the metaconid (lost in potoroines other than propleopines). The plesiomorphic balbarines, *Nambaroo*, *Wururoo* and *Gauwumaya* certainly

indicate that the protostylid has been reduced and ultimately lost in balbarines, however there is less evidence to support a belief that it has been retained in potoroines. The M_1 (Cooke, 1997) protostylid of *Palaeopotorous priscus* Flannery & Rich, 1986, bears a similar relationship to the protoconid and cristid obliqua as does that of *H. moschatus*, exhibiting a condition intermediate between the distinct cuspid of the protostylid of *Nambaroo* and the protostylid crest of *W. dayamayi*. It thus may represent an early stage in the reduction of the protostylid among potoroines. In the proposals of cusp homology in macropodids and potoroines referred to above, the condition occurring in *H. moschatus* is crucial because it is used in both cases to represent the intermediate condition between a phalangerid ancestor and more derived potoroines. If, as has been proposed here, the reduced cuspid from which the paracristid originates on the short M_1 protolophid of *H. moschatus* is the protoconid, then there is no reason to suppose that this is not also the case in other potoroines and the sequence, *Palaeopotorous* - *Hypsiprymnodon* - *Potorous*, used by Flannery & Rich (1986) to illustrate their argument can be taken as indicating a transition involving reduction of the protostylid.

The protostylid is also exhibited in varying degrees of development within phalangerids. A very similar structure to the M_1 protostylid crest of *W. dayamayi* occurs in *Phalanger intercastellanus* and joins the cristid obliqua. In *Trichosurus vulpecula* there is a straight ridge

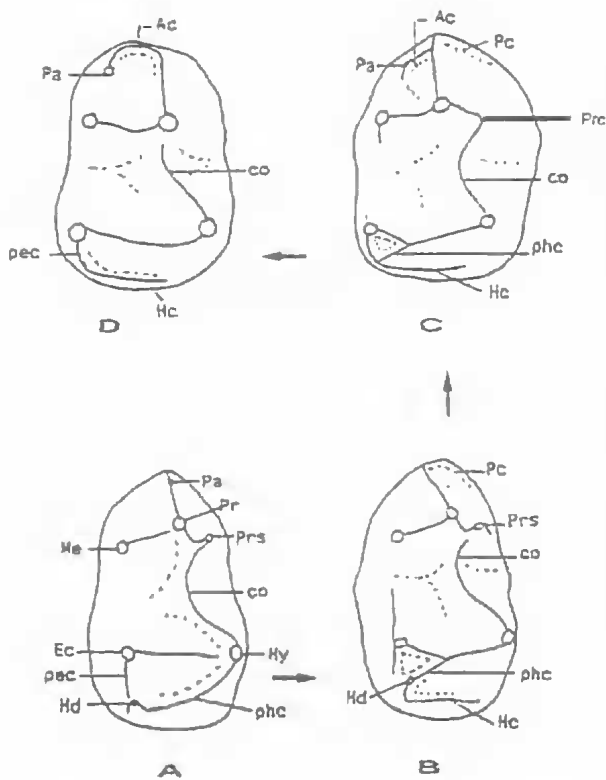


FIG. 7. Evolution of lower molar morphology in balbarines illustrated by RM_1 . A, hypothetical macropodoid ancestor. B, *Nambaroo couperi*. C, *Wururoo dayamai*. D, *Balbaroo* grade. Abbreviations: Ac=anterior cingulid; co=cristid obliqua; Ec=entocoid; Hc=hypoconulid; Hd=hypoconulid; Hy=hypoconid; Me=metaconid; Pa=paraconid; Pc=precingulid; pec=postentocristid; phc=posthypoconid; Pr=protoconid; Prs=protostylid; prc=protostylid crest.

descending posterobuccally to the base of the protoconid where it links to the cristid obliqua. In *T. caninus* there is a ridge on the protoconid resembling that in *T. vulpecula*, but it does not contact the cristid obliqua which independently ascends the posterior face of the protoconid. Flannery & Rich (1986) indicate a discrete protostylid in *Phalanger vestitus* and a similar situation occurs in *Spilogale maculatus*, but in some specimens of this species the protostylid may be reduced to a ridge on the posterobuccal flank of the protoconid. Flannery & Archer (1987) suggest a protostylid on M_1 in *Strigocuscus reidi* and *Trichosurus dicksoni*, both from System C sites at Riversleigh.

It would appear that the genetic potential for the formation of a protostylid is widespread among phalangeridans and may be considered as

plesiomorphic for the group. In pseudocheirids among *Petauroidea* and *Nambaroo* among *Macropodoidea* the protostylid is fully developed but in most phalangerids and in *Palaeopotorpus*, *Hypsiprinodon* and *Wururoo* the potential is not as fully expressed. This expression has independently been suppressed among more derived macropodoids (with the possible exception of propleopines) and other phalangeridans.

Wururoo is more derived than *Nambaroo* in terms of M_1 morphology: the protostylid has been reduced, a neomorphic anterior cingulid has begun to form and the trigonid basin has become partly enclosed. *Nambaroo* and *W. dayamai* indicate initial stages of a trend among balbarines towards the development of an anterior cingulid and the enclosure of the trigonid basin. Concomitant with this trend is a decrease in the relative importance of the precingulid which occupies much of the M_1 anterior margin in plesiomorphic species such as *N. couperi*.

Hypolophid formation in balbarines proceeded as outlined by Flannery & Rich (1986), involving elevation and lingual displacement of the posthypoconid which contributes a buccal component to the hypolophid, the lingual component contributed by a buccally directed cristid from the entoconid. The latter cristid is not necessarily a neomorphic 'entohypoconid' (Ride, 1993). However, the hypoconulid on the M_1 of *N. couperi* and its apparent presence in a reduced form on M_1 of *W. dayamai* indicates the additional involvement of this cuspid in hypolophid formation in plesiomorphic balbarines (Fig. 7).

The hypoconulid in such forms is contacted by a lingually displaced, diagonal posthypoconid. An inverted triangular fossette occurs on the lingual posterior face of the hypolophid, bounded by the posthypoconid and the postentocristid (when present). A shallow fossette develops buccal to the posthypoconid and a neomorphic cingulid, the hypoconulid according to the definition of Butler (1990), develops running transversely across the posterior base of the hypolophid from the hypoconulid or, when that structure has been lost, from the ventral end of the posthypoconid, as in *N. vultavus*. The posthypoconid is lost in more derived species such as those of *Balbaroo* in which the postentocristid links to a transverse,

posterior cingulid homologous with the hypocingulid.

The modification offered above to the hypothesis of Flannery & Rich has been extended by Ride (1993) to macropodoids in general but I apply it only to balbarines. The bilophodont lower molar morphology of bulungamayines is derived from a bunolophodont ancestral form by different means to those outlined above (Cooke, 1997) and clearly indicates independent evolution of lophodonty within this group. However, a hypoconulid positioned low on the posterior, lingual face of the hypolophid and associated with a posthypocristid, is the probable plesiomorphic condition for all macropodoids. The basal macropodoid may well have had a bunolophodont lower molar morphology similar to that of *Palaeopotoroides* or of phalangerids, but with a more distinct protostylid buccal to the protoconid and a hypoconulid contacted by the posthypocristid at the posterior base of the entoconid. The lingual component of the balbarine hypolophid would represent a reduction of the buccal cristid of the entoconid which forms the transverse posterior lophid of bunolophodont macropodoids.

The hypoconulid in plesiomorphic balbarines and its absence in any known potoroids of comparable age suggests that balbarines diverged early from the main stem of macropodoid evolution and independently and probably rapidly evolved lophodonty, the better to exploit a herbivore niche. The combination of plesiomorphic dental characters present in balbarines, including lateral compression of the M₁ trigonid and the presence of both a hypoconulid and protostylid on this tooth, contrasts markedly with the absence of such characters in bulungamayines. There has been parallel (and probably later) evolution of lophodonty within Bulungamayinae and the absence of plesiomorphic molar characters such as those indicated above, suggests that bulungamayines may be more likely to be ancestral to the highly derived macropodids.

ACKNOWLEDGEMENTS

Research grants from the Australian Research Council and the University of New South Wales have been the primary mechanism for providing the research material examined in this study. Additional support for the Riversleigh project has come from the National Estates Program grants, the Australian Geographical Society, The Australian Museum, The Riversleigh Society, ICI Pty

Ltd, Century Zinc Limited, the Mt Isa Shire and private donors.

I thank the Director and staff of the Queensland Museum for provision of workspace and facilities; Jeff Wright and Alex Cook for preparation of photographic prints; Michael Archer and David Ride for their helpful discussions; the staff and students at the University of New South Wales involved with the Riversleigh Project who have been so willing in their assistance.

LITERATURE CITED

- APLIN, K.P. & ARCHER, M. 1987. Recent advances in marsupial systematics with a new syncretic classification. Pp xv-lxxii. In Archer, M. (ed), *Possums and opossums: studies in evolution*. (Surrey Beatty & Sons: Sydney).
- ARCHER, M. 1978. The nature of the molar-premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheekteeth. *Memoirs of the Queensland Museum* 18: 157-164.
- ARCHER, M. & FLANNERY, T.F. 1985. Revision of the extinct gigantic rat kangaroos (Potoroidae: Marsupialia), with a description of a new Miocene genus and species and a new Pleistocene species of *Propleopus*. *Journal of Paleontology* 59: 1131-1149.
- ARCHER, M., GODTHELP, H., HAND, S.J. & MEGIRIAN, D. 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist* 25(2): 29-65.
- BREEN, G. 1981. The Mayi languages of the Queensland gulf country. *Australian Institute of Aboriginal Studies AIAS new series* 29.
- BUTLER, P.M. 1978. Molar cusp nomenclature and homology. Pp 439-453. In Butler, P.M. & Joysey, K. (eds), *Development, function and evolution of teeth*. (Academic Press: London).
1990. Early trends in the evolution of tribosphenic molars. *Biological Reviews* 65: 529-552.
- COOKE, B.N. 1992. Primitive macropodids from Riversleigh, northwestern Queensland. *Alcheringa* 16: 201-217.
1997. New Miocene bulungamayine kangaroos (Marsupialia, Potoroidae) from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41: 281-294.
- FLANNERY, T.F. 1989. Phylogeny of the Macropodoidea: a study in convergence. Pp 1-46. In Grigg, G., Jarman, P & Hume, I. (eds), *Kangaroos, wallabies and rat-kangaroos*. (Surrey Beatty & Sons: Sydney).
- FLANNERY, T. & ARCHER, M. 1987. *Strigocuscus reidi* and *Trichosurus dicksoni*, two new fossil phalangerids (Marsupialia: Phalangeridae) from the Miocene of northwestern Queensland. Pp 527-536. In Archer, M. (ed.), *Possums and opossums:*

- studies in evolution. (Surrey Beatty & Sons: Sydney).
- FLANNERY, T.F., ARCHER, M. & PLANE, M. 1982. Middle Miocene kangaroos (Macropodoidea: Marsupialia) from three localities in northern Australia, with a description of two new subfamilies. Bureau of Mineral Resources Journal of Australian Geology and Geophysics 7: 287-302.
- FLANNERY, T.F. & RICH, T.H.V. 1986. Macropodoids from the Middle Miocene Namba Formation, South Australia, and the homology of some dental structures in kangaroos. Journal of Paleontology 60(2): 418-447.
- FLOWER, W.H. 1867. On the development and succession of teeth in the Marsupialia. Philosophical Transactions of the Royal Society of London B157: 631-641.
- LUCKETT, W.P. 1993. An ontogenetic assessment of dental homologies in therian mammals. Pp 182-204. In Szalay, F.S, Novacek, M.J. & McKenna, M.C. (eds), Mammal phylogeny. (Springer-Verlag: New York).
- MYERS, T.J. & ARCHER, M. 1997. *Kuterinjangama* (Marsupialia, Illariidae): a revised systematic analysis based on material from the late Oligocene of Riversleigh, northwestern Queensland, Australia. Memoirs of the Queensland Museum 41: 379-392.
- RIDE, W.D.L. 1961. The cheek teeth of *Hypsiprimnodon moschatus* Ramsay 1876 (Macropodidae: Marsupialia). Journal and Proceedings of the Royal Society of Western Australia 44: 53-60.
1993. *Jackmahoneya* gen. nov. and the genesis of the macropodiform molar. Memoirs of the Association of Australasian Palaeontologists 15: 441-459.
- SZALAY, F.S. 1969. Mixodectidae, Microsyopidae, and the Insectivore-Primate transition. Bulletin of the American Museum of Natural History 140: 193-330.
- VAN VALEN, L. 1966. Deltatheridia, a new order of mammals. Bulletin of the American Museum of Natural History 132: 1-126.
1994. Serial homology: the crests and cusps of mammalian teeth. Acta Palaeontologica Polonica 38, 3/4: 145-158.
- WOODBURNE, M.O., MACFADDEN, B.J., CASE, J.A., SPRINGER, M.S., PLEDGE, N., POWER, J.D., WOODBURNE, J.M. & SPRINGER, K.B. 1993. Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (late Oligocene) of South Australia. Journal of Vertebrate Paleontology 14: 483-515.